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Model for the Examination of Evolutionary Trends in Tooth Development

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ABSTRACT Through the use of serial computerized tomography (C-t) scans, two distinct developmental stages can be identified in mature teeth. C-t scans thus provide a non-destructive method for assessing growth within individual teeth, as well as for comparison of the development of modern and fossil teeth. The second deciduous molar (DM2) and first permanent molar (M1) resemble one another morphologically, despite differences in size and developmental rates. Thus, they provide an excellent model for studying variation in growth within an individual. To test the C-t method, we first examined a recent archaeological sample and then examined teeth from Skhul I.

Serial C-t scans were used to compare two distinct developmental stages represented by the dentine-enamel junction (DEJ) and outer enamel surface (OES), respectively, in mandibular DM2 and M1 of 31 archaeological specimens. The difference in form and size between these two surfaces in and between teeth was calculated from intercusp distances measured at the DEJ and OES using the form distance matrix. Intercusp distances at the DEJ and OES of these teeth were then compared to their counterparts in the DM2 and M1 of Skhul I, taken here as representative of early anatomically modern *Homo sapiens sapiens*.

Form differences between paired DM2 and M1 at the DEJ were smaller than those at the OES, supporting the hypothesis that differences between the two teeth increase throughout development. The increase in intercusp distances from the DEJ to OES was found to reflect the angulation of cusps relative to one another, rather than enamel thickness. Form differences between the Skhul DM2 and M1 were smaller than those observed in the recent series, and the recent M1 differed more than the DM2 from its fossil counterpart. The similarities found between the Skhul permanent and deciduous teeth and the recent DM2, may reflect a similar growth pattern. This would contribute to earlier crown completion in the fossil M1. Am. J. Phys. Anthropol. 102:283–294, 1997 © 1997 Wiley-Liss, Inc.

The last decade has seen renewed interest in the early development of fossil hominids, with most studies focussing on dental growth rates assessed from microscopic studies of enamel prisms, striae of Retzius and perikymata (Beynon, 1992; Bromage and Dean, 1985; Dean et al., 1986, 1993; Mann et al., 1990; Ramirrez-Rozzi, 1993). Little attention has been given to dental morphogenesis, although the dentine-enamel junction (DEJ) preserved in adult teeth represents

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an early stage of odontogenesis. We propose that the DEJ can be accurately identified from serial computertised tomography (C-t) scans, thus enabling us to compare, in a non-destructive fashion, similar stages of development in fossil and recent teeth irrespective of the chronological age of the specimen at death. Here we develop this model in two steps. Serial C-t scans were used to compare early and late stages of dental development in the second deciduous molar (DM2) and first permanent molar (M1) of a recent archaeological sample and DM2 and M1 in the Skhul I mandible.

Dental development

It is generally accepted that traits that develop early in ontogeny are those that are the most archaic phylogenetically (Alberch, 1980; Alberch et al., 1979; Gould, 1989; Sofaer, 1973). New traits or modifications of archaic traits can be related to localized modification of growth rates, according to the "clock model" presented by Gould (1977) and elaborated upon by Alberch et al. (1979). This concept has been widely utilized in comparative studies of developmental processes in primitive vertebrates (Alberch, 1980; Gould, 1989; Wagner, 1989), but has obvious limitations for the longitudinal study of fetal development in mammals. In this context the dentition constitutes a unique source of information on developmental processes. Dental development in mammals is initiated at an early stage of embryonic differentiation, and with few exceptions, such as rat incisors, is of limited duration. The meristic pattern of tooth formation means that teeth within each tooth group, such as molars, premolars and incisors, represent sequential phases of development of the same basic tooth type. Since they develop at different ages, they provide "serial data" representative of different developmental ages within one individual (Butler, 1956, 1967a,b, 1971; Dahlberg, 1945, 1985; Kraus and Jordan, 1965; Saunders and Mayhall, 1982; Sofaer et al., 1972; Smith, 1989; Smith et al., 1987, 1988). Moreover, each tooth retains a permanent record of two successive phases of development, that can be easily identified on radiographs or C-t scans because of their different densities. There is an early stage, representing the tooth germ defined by the DEJ, and a later stage defined by the OES.

Dental ontogeny has been studied for at least a hundred years, but much of our knowledge of the successive stages of morphogenesis and patterns of development of different tooth groups in humans is based on studies carried out by Butler (1967a,b, 1968, 1971) and Kraus (1952, 1963) and Kraus and Jordan (1965) in the 1950s and 1960s. These researchers used intact tooth germs dissected out of the jaws of aborted fetuses, to measure and record the overall pattern of cusp formation, size increase and calcification. From these tooth germs, Kraus and Jordan (1965) described the three dimensional appearance of tooth germs from the bell stage, that is, the presence of a unicusped mound, to advanced stages of enamel matrix formation in all the deciduous teeth, and the initial stage of calcification of the M1.

These studies also confirmed that enamel formation in the deciduous molars and M1 begins on the protoconid in the lower molars, and the paracone in the upper molars. Cell proliferation and furrow formation continue in adjacent regions, so that the relative height and distance between cusps may change, and additional cusps and invaginations appear following the onset of calcification. In the DM2, mineralization begins at around 5 months in utero, before all cusps are well defined, so that morphogenesis and mineralization proceed simultaneously. In the M1, mineralization begins at around 28 weeks in utero, when all cusps are well defined, and proceeds at a slower rate than in the DM2. In all teeth, the DEJ only achieves its final form when all centers of calcification have united. The order of calcification has been found to be more regular in the DM2 than in the slower growing M1 (Butler, 1967b; Kraus and Jordan, 1965).

Destructive and non-destructive methods for the study of dental development

Information on the relationship between the DEJ and OES of the same tooth has been obtained from two types of study. Kraus (1952) measured intercusp distances at the

OES of lower first molars, dissolved away the enamel, and then measured intercusp distances at the exposed DEJ. The same approach was used by Sakai (1974) and others to compare the OES and DEJ of other tooth types in humans and other species. Korenhof (1960, 1963, 1982) examined a large series of teeth, recovered from archaeological excavations, in which the dentine had dissolved, leaving only the enamel caps. He made casts of the internal surface of these caps, which gave him a three dimensional outline of the DEJ and compared this with the intact OES of the same tooth. The "longitudinal" data so obtained demonstrated differences between the two surfaces that varied between teeth in accordance with the field theory of Butler (1956) and the findings obtained from cross-sectional studies of tooth germs (Kraus and Jordan, 1965). The extent to which the surface represented at the DEJ differed from that represented at the OES in cusp number and furrows increased in later developing teeth, and showed least change in the early developing key teeth (Dahlberg, 1945, 1985).

The two distinct stages of tooth formation represented by the DEJ and OES that can be identified in the completed tooth provide a two stage model of development within any one tooth that constitutes a unique system for comparing ontogenetic processes in both fossil and contemporary specimens. However, since the method used by Kraus (1952), Korenhof (1960, 1963, 1982) and Sakai (1974) involved destruction of part of the tooth, it obviously could not be applied to studying ontogenetic processes in rare fossil teeth.

C-t affords an alternative and non-destructive approach to the visualization and comparison of the external and inner surfaces of different objects. Developed as an aid in medical diagnosis, it provides an accurate view of internal structures along selected planes, or alternately, serial views can be superimposed to provide three-dimensional reconstruction. Measurements based on these three dimensional reconstructions have been found to be sufficiently accurate for the construction of precise prostheses for insertion during surgery (Pirairo et al., 1993), as well as for metric analysis of fossil skulls (Zollikofer et al., 1995). Spoor et al. (1993) compared serial C-t scans with ground sections of the same tooth and found the maximum error range for enamel thickness to be of the order of ± 0.1 mm. The main problem encountered is the difficulty of obtaining a window setting that will minimize the bias caused by the different densities of the enamel-air and enamel-dentine boundaries. This may be minimized either by using different window settings for each boundary, or by using a fixed window centered to minimize the distortion. In this case, the bias is constant and a relative rather than absolute value is obtained that is adequate for comparison of samples analyzed in the same way. Thus, using a fixed window, Smith et al. (1993) found good concordance (differences averaging 3%) between three dimensional measurements taken at the DEJ of a tooth reconstructed from serial C-t scans taken at 1 mm intervals, and those taken directly at the DEJ of the same tooth after decalcification of enamel.

This study

In the present study, we have used serial C-t scans to quantify the difference between cuspal morphology at the DEJ and OES of the lower DM2 and M1. These data were used to evaluate differences in ontogeny of the two teeth and to develop a model for the study of developmental processes and evolutionary trends in the hominid dentition.

MATERIALS AND METHODS

Assessment in recent archaeological remains

Mandibles of 31 infants recovered from archaeological excavations in Israel and dated between 6000 B.P. and 200 A.D. were used in the first part of this study. Selection was based on an estimated dental age of 3–6 years and the presence of an unworn DM2 and unerupted M1 with at least three-fourths of the crown complete. Serial C-t scans were then taken in the bucco-lingual plane of the lower DM2 and M1. The C-t scans were made using an Elscint 2400 model, with scans 1.2 mm thick, but taken at 0.5 mm intervals to give intercalated

scans. On these scans x and y coordinates were registered for cusp tips at the DEJ and OES (Fig. 1), using a work station and optimizing window settings for each reading (i.e., separate readings for the enamel-air and enamel-dentine boundaries). The third coordinate, z, was calculated from the distance between successive slices. All scans were remeasured at least twice on separate occasions and values averaged. Where differences exceeded 3%, teeth were rescanned and if easily duplicable measurements could not be obtained they were excluded from analysis. When all scans of any one tooth had been examined in this way, the coordinates for the peaks of each of the five main cusps at the OES and DEJ were entered into the data base. This gave 10 landmarks for each tooth, the five cusp tips at the DEJ and the same five cusp tips represented at the OES. The Euclidean distance matrix (EDMA) was calculated between all landmarks to provide a form-free three dimensional grid for each tooth that could be visualized from different angles. The difference in form and size expressed by intercusp distances at the DEJ and OES of each tooth was then calculated using the Form Distance Matrix (Corner and Richtsmeier, 1992; Lele, 1991; Lele and Richtsmeier, 1992). The form distance matrix gives the ratio of the two surfaces that are being compared. Thus, the DEJ and OES will have the same form (i.e., same shape and size) if all values are 1, and the same shape if all values change by the same constant.

The significance of differences between intercusp distances of the two surfaces with a fixed relationship to one another within and between teeth was examined using one-way paired t-tests. Specifically, the one-tailed t-tests were used to evaluate the significance of increases in intercusp distances from the DEJ to the OES of each tooth, and to determine the significance of increased intercusp distances at the DEJ and OES of the M1 relative to the DM2 of the same individual. A graphic estimation of differences between teeth was made using the GRF program developed by Rohlf and Slice (1990) for least mean squares analysis.

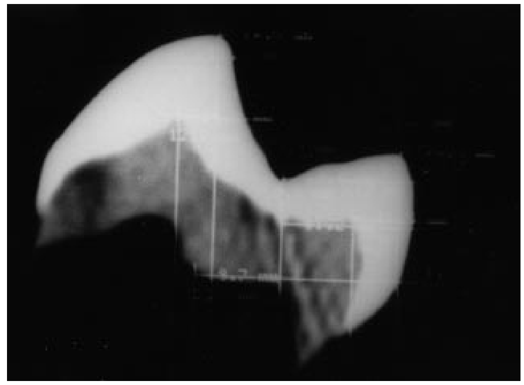

Fig. 1. One slice of a tooth as shown by C-t scan. Note the X and Y coordinates used for defining cusp tips. Z coordinate defined by the amount the tooth advanced between slices.

Application to fossil specimens

The mandible of Skhul I dated to circa 90,000 B.P., was used as an example of early *Homo sapiens sapiens*, with molars in place. C-t scans and all statistical analyzes used the statistical tests described for the Holocene infant mandibles. Finally, comparisons were made between the Skhul I and Holocene teeth.

RESULTS

Holocene specimens

Tables 1a and 1b present the mean value and variance calculated for intercusp distances at the DEJ and OES of the 31 paired DM2s and M1s. Symbols used in the tables and text are as follows: protoconid (Pd); metaconid (Md); entoconid (Ed); hypoconulid (Hd) and hypoconulid (Hyd). In addition, where reference is made specifically to cusp tips at the DEJ, the suffix d (dentine) is used, and for cusp tips at the OES the suffix e (enamel) is used. In the DM2, 9/10 intercusp distances at the OES were significantly greater than those measured at the DEJ ($P < 0.001$ for 8 values and $P = 0.02$ for the ninth, the Pd-Hd distance. The Md-Ed distance was the only one to show no significant increase. In the M1, 9/10 intercusp distances at the OES were significantly greater than those measured at the DEJ ($P < 0.001$), but here the exception was the Pd-Hd distance. All intercusp distances in the M1 were sig-

TABLE 1a. The Euclidean distance matrix between cusp tips in DM2[1]

Mean										
Hydd[2]	0.00									
Hdd	27.57	0.00								
Pdd	59.42	34.30	0.00							
Edd	35.98	44.71	59.31	0.00						
Mdd	62.37	48.51	32.89	42.89	0.00					
Hyde	11.69	29.28	61.25	40.90	66.06	0.00				
Hde	32.82	11.67	33.91	47.96	49.60	30.60	0.00			
Pde	64.58	39.25	11.10	64.69	37.49	64.67	35.75	0.00		
Ede	40.58	47.93	60.98	11.73	43.75	42.54	48.46	64.57	0.00	
Mde	65.94	52.00	35.70	46.01	12.23	67.79	50.48	36.97	43.90	0.00
	Hydd	Hdd	Pdd	Edd	Mdd	Hyde	Hde	Pde	Ede	Mde
Variance										
Hydd	0.00									
Hdd	22.45	0.00								
Pdd	29.07	21.69	0.00							
Edd	21.01	17.33	26.82	0.00						
Mdd	24.68	22.64	10.84	21.48	0.00					
Hyde	8.06	30.30	44.02	26.04	43.25	0.00				
Hde	24.28	7.13	29.01	17.43	29.12	26.67	0.00			
Pde	38.72	22.87	6.26	37.10	13.97	45.76	25.41	0.00		
Ede	23.36	20.72	31.63	5.80	28.45	32.11	20.82	39.56	0.00	
Mde	36.81	28.07	15.98	20.89	4.33	50.67	33.54	18.49	29.91	0.00
	Hydd	Hdd	Pdd	Edd	Mdd	Hyde	Hde	Pde	Ede	Mde
Variance										

[1]Thirty-one second deciduous molars were examined.
[2]Key: Hyd, hypoconulid; Md, metaconid; Hd, hypoconid; Ed, entoconid; Pd, protoconid; d, dentine; e, enamel. Units are in 1/10 mm. Using one-tailed paired t-tests, a significant increase was found in all intercusp distances at the outer enamel surface, except for the Md-Ed distance ($P < 0.001$ for 8 and $P < 0.02$ for 1).

TABLE 1b. The Euclidean distance matrix between cusp tips in M1[1]

Mean										
Hydd[2]	0.00									
Hdd	25.84	0.00								
Pdd	63.44	41.49	0.00							
Edd	38.22	50.10	67.33	0.00						
Mdd	71.18	62.37	42.32	50.62	0.00					
Hyde	18.98	32.36	68.84	45.04	77.31	0.00				
Hde	34.41	19.85	46.00	54.99	66.05	28.85	0.00			
Pde	66.01	43.87	16.93	71.30	48.46	66.81	40.88	0.00		
Ede	44.97	55.84	72.33	18.25	54.94	43.91	54.23	72.25	0.00	
Mde	77.48	68.70	48.43	56.11	16.78	79.87	67.62	49.21	55.02	0.00
	Hydd	Hdd	Pdd	Edd	Mdd	Hyde	Hde	Pde	Ede	Mde
Variance										
Hydd	0.00									
Hdd	25.91	0.00								
Pdd	15.34	27.15	0.00							
Edd	38.63	15.77	24.02	0.00						
Mdd	18.76	32.32	15.18	20.59	0.00					
Hyde	11.34	35.85	19.87	36.20	21.03	0.00				
Hde	24.98	8.56	19.16	18.44	32.86	37.30	0.00			
Pde	31.83	29.03	7.85	32.05	20.99	39.24	29.99	0.00		
Ede	23.19	21.54	23.96	10.28	19.21	38.19	24.17	36.76	0.00	
Mde	33.17	46.01	26.57	42.02	7.27	46.69	50.31	36.31	39.64	0.00
	Hydd	Hdd	Pdd	Edd	Mdd	Hyde	Hde	Pde	Ede	Mde

[1] Thirty-one first permanent molars were examined.
[2] Key: Hyd, hypoconulid; Md, metaconid; Hd, hypoconid; Ed, entoconid; Pd, protoconid; d, dentine; e, enamel. Units are in 1/10 mm. Using one-tailed paired t-tests, a significant increase was found in all intercusp distances at the outer enamel surface (OES) ($P < 0.001$) except for the Pd-Hd distance.

nificantly greater than homologous distances in the DM2, with the exception of the Hd-Hyd and Pd-Hd.

In both teeth, the mean test statistic, T, calculated from the ratios of distances at the DEJ to OES in the DM2 was very similar to that of M1 (1.19 and 1.17 respectively, Table 2). Since we were looking at changes in form within individual teeth and between pairs of teeth derived from the same specimen, the

TABLE 2. Ranked form difference matrix calculated from the ratio between Euclidean intercusp distance measurements at the DEJ and OES of M1 and DM2[1]

M1				DM2			
Cusps		Ratio	variance	Cusps		Ratio	variance
Pd[2]	Hd	0.99	0.02	Md	Ed	1.03	0.01
Pd	Hyd	1.05	0.01	Md	Hd	1.04	0.00
Ed	Pd	1.07	0.00	Pd	Hd	1.05	0.02
Ed	Hd	1.08	0.00	Ed	Hd	1.09	0.00
Md	Hd	1.08	0.00	Md	Hyd	1.09	0.00
Md	Ed	1.09	0.01	Pd	Hyd	1.09	0.00
Hd	Hyd	1.12	0.02	Ed	Pd	1.09	0.00
Md	Hyd	1.12	0.01	Hd	Hyd	1.12	0.02
Md	Pd	1.16	0.01	Md	Pd	1.12	0.00
Ed	Hyd	1.16	0.02	Ed	Hyd	1.19	0.01

[1] Note the difference in order of ranking of ratios in the two teeth. The test statistic, T, calculated from the form distance matrix between the outer enamel surface (OES) and dentin-enamel junction (DEJ) for M1 = 1.19; for DM2 = 1.17.
[2] Key: Hyd, hypoconulid; Md, metaconid; Hd, hypoconid; Ed, entoconid; Pd, protoconid; d, dentine; e, enamel. Units are in 1/10 mm.

variance of T was used to assess the significance of the deviation of T values from 1. As can be seen from Table 2, both teeth showed a small but significant change in form between the DEJ and OES. Further, the rank order of the differences found varied in the two teeth, indicating shape differences in growth patterns between them, as demonstrated in Figure 2. This is further shown in Table 3, which presents the form difference matrix for comparisons made between homologous distances in each pair of DM2 and M1, and the T ratios for comparisons between the DEJ and OES of the two teeth. The form differences between the paired teeth increase from the DEJ to OES (T = 1.3 and 1.6, respectively) supporting the hypothesis that the two teeth show a greater resemblance in earlier than in later stages of development. The mean T value for all distances in the two teeth was 1.81. As can be seen from Tables 1 and 2, the distance between the OES and DEJ of individual cusps in the DM2 was approximately two-thirds that of the distance between enamel and dentine cusp tips in the M1, a finding which agrees well with the expected difference in enamel thickness between the two teeth.

In both teeth, the distance between dentine and enamel tips of homologous cusps was least for the protoconid. In the DM2 the other four cusps showed relatively little difference. In the M1 there was a tendency towards an increase in the distance between the enamel and dentine cusp tips of the distal cusps.

Fossil specimens

In the Skhul I DM2, cusp tips at the OES were slightly abraded but repeated scans gave consistent readings. The form difference matrix differed from that of the recent DM2 in that three intercusp distances measured at the OES were similar or smaller than those measured at the DEJ (Pd-Hd, Md-Hd and Md-Ed). A similar pattern was seen in the Skhul M1 where the Pd-Hd and Md-Hd distances were smaller at the OES than at the DEJ and the Md-Ed distance showed no change. In both teeth, the largest increase in intercusp distance from the DEJ to OES was found between Hyd-Hd. All intercusp distances in the Skhul M1 were larger than those in the Skhul DM2. T values calculated between these teeth were 1.22 at the DEJ and 1.20 at the OES (Table 4).

All intercusp distances in the infant Holocene DM2 were smaller than those of the Skhul DM2, but the teeth were similar in form with T values of 1.17 at the DEJ and 1.33 at the OES. The Holocene M1 and Skhul M1 differed more than the deciduous teeth, with T values of 1.4 at the DEJ and 1.63 at the OES (Table 5). The main differences were in Hd-Hyd, Pd-Hd and Ed-Md ratios, which showed an opposite trend. In the fossil tooth the Hd-Ed-Hyd triangle was large relative to the rest of the tooth; in the Holocene M1 this triangle was reduced, and the tooth was more rectangular in form with an expanded Pd-Hd and Hd-Md distance. The main direction of changes found is shown graphically in Figure 3, where least mean squares analysis was used to show the overall change in shape between the Skhul M1 and each of the Holocene samples.

DISCUSSION

The morphological resemblances observed between the DM2 and M1 reflects their common developmental origin within the same tooth district. DM2, the earlier and more rapidly developing tooth, is considered to be more conservative in form from an evolutionary perspective than the M1 (Butler, 1956, 1971; Dahlberg, 1945; Saunders and Mayhall, 1982; Suzuki and Sakai, 1973).

TABLE 3. The mean form difference between homologous cusps in paired DM2 and M1 ranked in ascending order[1,2]

From	To	Distance	Variance	From	To	Distance	Variance
Hdd[3]	Hydd	0.98	0.12	Hyde	Mdd	1.18	0.02
Hde	Hyde	0.99	0.14	Mde	Hyde	1.19	0.02
Pde	Hydd	1.03	0.02	Ede	Pdd	1.19	0.01
Ede	Hyde	1.04	0.03	Mdd	Edd	1.19	0.02
Pde	Hyde	1.05	0.03	Pdd	Hdd	1.22	0.02
Hde	Hydd	1.07	0.04	Mde	Edd	1.23	0.03
Pdd	Hydd	1.08	0.01	Mde	Ede	1.27	0.04
Edd	Hydd	1.08	0.04	Ede	Mdd	1.27	0.03
Pde	Edd	1.11	0.01	Mdd	Hdd	1.29	0.01
Hyde	Edd	1.11	0.03	Mdd	Pdd	1.29	0.01
Ede	Hydd	1.12	0.02	Pde	Mdd	1.30	0.01
Ede	Hde	1.12	0.01	Mde	Hdd	1.33	0.02
Ede	Pde	1.13	0.01	Mde	Pde	1.34	0.02
Edd	Hdd	1.13	0.01	Hde	Mdd	1.34	0.01
Pde	Hdd	1.13	0.02	Mde	Hde	1.35	0.02
Hyde	Pdd	1.14	0.03	Mde	Pdd	1.37	0.02
Edd	Pdd	1.14	0.01	Hde	Pdd	1.38	0.04
Mdd	Hydd	1.15	0.01	Mde	Mdd	1.40	0.08
Hde	Edd	1.15	0.01	Pde	Pdd	1.59	0.16
Pde	Hde	1.16	0.04	Ede	Edd	1.63	0.21
Ede	Hdd	1.17	0.01	Hyde	Hydd	1.70	0.18
Hyde	Hdd	1.18	0.22	Hde	Hdd	1.79	0.24
Mde	Hydd	1.18	0.01				

[1] Using one-tailed paired t-tests for comparison between homologous cusps in the DM2 and M1, all intercusp distances were significantly larger in M1 than in DM2, except for the Pd-Hd and Hd-Hyd.
[2] T-values between the two teeth were statistically significant: DEJM1/DEJDM2 = 1.3; OESM1/OESDM2 = 1.66.
[3] Key: Hyd, hypoconulid; Md, metaconid; Hd, hypoconid; Ed, entoconid; Pd, protoconid; d, dentine; e, enamel. Units are in 1/10 mm.

That is, it retains the conservative Dryopithecine 5Y pattern, considered characteristic of early hominids, as well as the great apes, even when the cusp pattern on the permanent molars is modified or the hypoconulid is lost (Hellman, 1928; Dahlberg, 1961). In this study we have used a three part model to examine this hypothesis. First, we compared early and late stages of development within the DM2 and M1, respectively; second, we compared similar stages of development between the DM2 and M1 in the same individuals, and third, we compared both early and late stages of development in each tooth with similar stages of development in the homologous teeth of a fossil hominid (Skhul I).

Cross-sectional studies previously carried out on the occlusal morphology of developing tooth germs (Coughlin and Christensen, 1966; Kraus and Jordan, 1965), like those based on comparison of the DEJ and OES of individual teeth following decalcification (Kraus, 1952; Korenhof, 1960), have emphasized that the hypoconulid is consistently present at the DEJ of the M1. Its loss or modification at the OES of the M1 has been attributed to local variations in the amount of enamel laid down. This modified or obliterated the boundaries between cusps defined at the DEJ. The thicker enamel and slower rate of formation of the M1 relative to the DM2, were considered to contribute to this phenomenon. However, in none of these studies was it possible to study directly the relationship of the DEJ to the OES within individual teeth. The three dimensional data retrieved from the serial C-t scans in this study provide for the first time a direct morphometric comparison of two distinct stages of development within individual teeth. The data indicate that the changes observed between the DEJ and OES, as expressed in intercusp distances, are not primarily related to enamel thickness, but rather to the angulation of the cusps relative to one another.

Butler (1968) measured intercusp distances of molar tooth germs in different stages of mineralization and reported that in the lower DM2, cusp tips tilted away from one another before being united by the coalescence of separate centers of mineralization. This he ascribed to continued rapid mitosis at the base of the developing cusps immediately prior to bridging. Butler (1967b), also found that in the upper DM2 enamel, apposition in the mesial cusp tips occurred before the soft tissue outline of the distal cusps was completed, so that the two

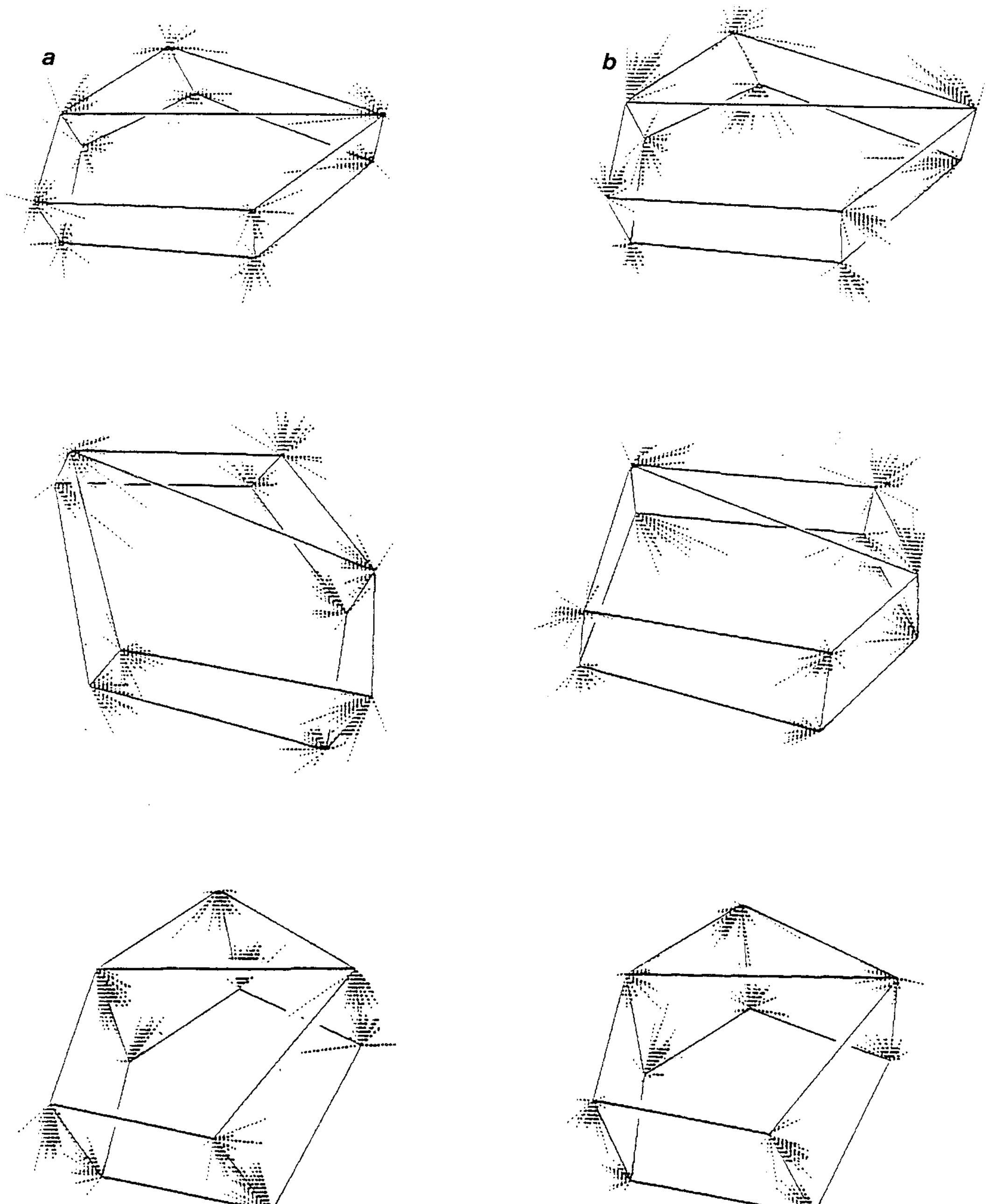

Fig. 2. Three dimensional reconstruction of three different views of DM2 and M1, each superimposed on the M1 of Skhul I using least mean square analysis. Note the differences in the length and direction of vectors (dotted lines) of the two tooth types. **a:** DM2. **b:** M1.

processes of morphogenesis and enamel apposition proceeded in step. This differed from the pattern of growth of the upper M1 where no calcification occurred before all cusps were completely delineated. These observations were based on prenatal to term specimens, and there is little published information on the later order of cuspal mineral-

TABLE 4. The Euclidean distance matrix for intercusp distances in Skhul I[1]

a) Between cusp tips at the OES											
DM2						M1					
Hyd[2]	0.00					Hyd	0.00				
Hd	37.01	0.00				Hd	43.08	0.00			
Pd	71.20	35.92	0.00			Pd	77.63	38.49	0.00		
Ed	50.54	61.09	75.83	0.00		Ed	55.23	69.68	80.62	0.00	
Md	71.13	52.59	41.26	46.97	0.00	Md	84.35	67.74	50.53	51.82	0.00
	Hyd	Hd	Pd	Ed	Md		Hyd	Hd	Pd	Ed	Md
b) Between cusp tips at the DEJ											
Hyd	0.00					Hyd	0.00				
Hd	33.20	0.00				Hd	37.22	0.00			
Pd	65.99	35.96	0.00			Pd	76.75	45.62	0.00		
Ed	43.01	54.97	67.86	0.00		Ed	47.28	65.28	79.78	0.00	
Md	68.59	53.49	37.01	46.42	0.00	Md	79.39	69.78	49.66	52.01	0.00
	Hyd	Hd	Pd	Ed	Md		Hyd	Hd	Pd	Ed	Md
The form difference matrix											
Hyd	1.00					Hyd	1.00				
Hd	1.11	1.00				Hd	1.16	1.00			
Pd	1.08	1.00	1.00			Pd	1.01	0.84	1.00		
Ed	1.17	1.11	1.12	1.00		Ed	1.17	1.07	1.01	1.00	
Md	1.04	0.98	1.11	1.01	1.00	Md	1.06	0.97	1.02	1.00	1.00
	Hyd	Hd	Pd	Ed	Md		Hyd	Hd	Pd	Ed	Md
T = 1.17						T = 1.38					

[1] Note the relative approximation of the protoconid and hypoconid at the outer enamel surface (OES) of Skhul I.
[2] Key: Hyd, hypoconulid; Md, metaconid; Hd, hypoconid; Ed, entoconid; Pd, protoconid; d, dentine; e, enamel. Units are in 1/10 mm.

ization and coalescence in the M1. Our results confirm that the form differences present in the DM2 and M1 at the early stages of mineralization increase in the later stages of enamel and dentine apposition. The results also show that the cusp pattern observed at the OES primarily reflects the angulation of the cusp tips relative to one another at the DEJ and we propose that this reflects mitotic rates at the base of cusps as described by Butler (1967a,b, 1968). Thus, approximation of the hypoconulid and hypoconid in the M1 indicates decreased mitosis at the base of these cusps relative to that observed between other cusps.

Developmentally the hypoconulid is the last cusp to appear and reduction or loss of the hypoconulid in hominids is associated with reduction in tooth size (Dahlberg, 1945, 1961). Since M1s in these smaller toothed populations take as long to develop as those of larger toothed populations (Fanning and Moorrees, 1969), there may be an inverse ratio between size and rate of development. The data presented here further indicate that this growth lag is most pronounced in the later phases of mitosis as represented by the last cusp to appear developmentally, the hypoconulid.

While one specimen cannot obviously be considered representative of early *Homo sapiens sapiens,* previous studies have found Skhul I to fall well within the average values for anatomically modern humans in size, morphology and developmental pattern (Smith and Arensburg, 1977; Skinner and Sperber, 1982; Tillier, 1992), and to differ from those of Neanderthals in tooth components (Zilberman et al., 1992; Faerman et al., 1994). We have accordingly used Skhul I to provide a preliminary estimate of possible developmental and evolutionary trends within *Homo sapiens sapiens.*

The results obtained from the serial C-t scans show that the Skhul DM2 and M1 are more similar to one another in form at the DEJ than are their modern counterparts, and that these resemblances are maintained at the OES. If cuspal form is indeed a reflection of differential rates of mitosis within the developing tooth, then it would appear that growth rates in the Skhul M1

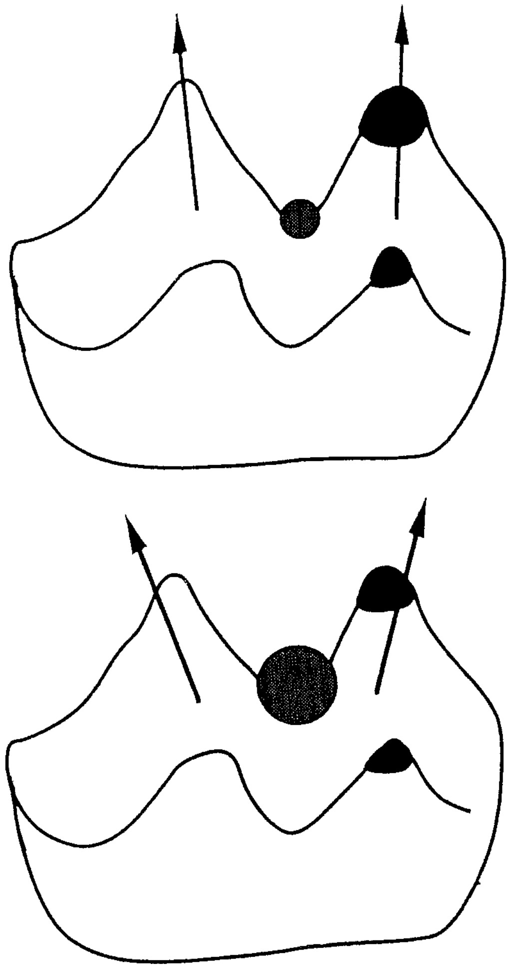

Fig. 3. Diagram showing the proposed relation between growth rates and angulation of cusps to one another in the DM2 and M1. Angulation increases with rapid localized growth, decreases with slower more generalized growth.

TABLE 5. The form difference matrix between Skhul I and recent[1] molars

a) Outer enamel surface (OES) in Fossil and Recent M1						
Hyd[2]	1.00					T
Hd	0.66	1.00				1.63
Pd	0.86	1.06	1.00			
Ed	0.79	0.77	0.89	1.00		
Md	0.80	0.99	0.97	1.08		
	Hyd	Hd	Pd	Ed	Md	
b) Dentine-enamel junction (DEJ) in Fossil and Recent M1						
Hyd	1.00					1.40
Hd	0.69	1.00				
Pd	0.82	0.90	1.00			
Ed	0.80	0.76	0.84	1.00		
Md	0.89	0.89	0.85	0.97	1.00	
	Hyd	Hd	Pd	Ed	Md	
c) OES in Fossil and Recent DM2						
Hyd	1.00					1.33
Hd	0.82	1.00				
Pd	0.90	0.99	1.00			
Ed	0.84	0.79	0.85	1.00		
Md	0.95	0.95	0.89	0.93	1.00	
	Hyd	Hd	Pd	Ed	Md	
d) DEJ in Fossil and Recent DM2						
Hyd	1.00					1.17
Hd	0.83	1.00				
Pd	0.90	0.95	1.00			
Ed	0.83	0.81	0.87	1.00		
Md	0.90	0.90	0.88	0.92	1.00	
	Hyd	Hd	Pd	Ed	Md	
e) OES in Fossil DM2 and M1						
Hyd	1.00					1.20
Hd	1.16	1.00				
Pd	1.09	1.07	1.00			
Ed	1.07	1.14	1.06	1.00		
Md	1.18	1.28	1.22	1.10	1.00	
	Hyd	Hd	Pd	Ed	Md	
f) DEJ in Fossil DM2 and M1						
Hyd	1.00					1.22
Hd	1.12	1.00				
Pd	1.16	1.26	1.00			
Ed	1.09	1.18	1.17	1.00		
Md	1.15	1.30	1.34	1.12	1.00	
	Hyd	Hd	Pd	Ed	Md	

[1] This study.
[2] Key: Hyd, hypoconulid; Md, metaconid; Hd, hypoconid; Ed, entoconid; Pd, protoconid; d, dentine; e, enamel. Units are in 1/10 mm.

and DM2 resembled one another more than do those of recent populations.

Comparison of the Skhul and recent molars further indicates that the recent DM2 resembles the Skhul DM2 and M1 more than it does the recent M1. These findings are in accordance with the hypotheses given at the beginning of the discussion, which considers the DM2 the more conservative tooth. The pattern of change in form observed, both temporally, as well as odontogenetically, indicates that in recent populations the M1 has changed more than the DM2. The form differences found between the Skhul M1 and the recent M1 suggest relatively more growth in the recent M1 in the trigonid at the expense of the talonid, the reverse of the pattern seen in the Skhul M1. That is, the recent M1 shows reduced growth of the distal moiety of the tooth.

Dental development in fossil hominids appears to have occurred faster (Beynon and Dean, 1987; Beynon and Wood, 1987; Conroy and Vannier, 1987; Dean et al., 1986; Smith, 1991; Ramirrez-Rozzi, 1993), if not at the same rate (Mann et al., 1990) as in modern smaller toothed humans. Certainly,

in living populations, larger teeth must develop faster than smaller teeth, since there appears to be no significant interpopulation difference in the timing and duration of crown development in the first and second permanent molars (Fanning and Moorrees, 1969), despite the large differences observed in tooth size. Proposals put forward to explain rapid development of large fossil teeth include increased rates of differentiation leading to rapid extension of the enamel front, with more ameloblasts functioning at the same time as well as an increased rate of activity of individual ameloblasts (Beynon, 1992; Beynon and Wood, 1986; Bromage and Dean, 1985; Dean et al., 1993; Grine and Martin, 1988). This characterizes the pattern of growth of modern deciduous teeth, in which enamel extension rates may be five times greater than those of the permanent molars (Shellis, 1984).

Can we go one step further and introduce an additional factor, that would associate rates of crown completion with cuspal morphology? Obviously no firm conclusions can be derived from the two teeth from Skhul I studied here. However, in its external morphology, the Skhul I specimen can certainly be considered typical of the conservative Y-shaped lower M1. If this is taken as a standard and we concede that external morphology reflects early development, then morphogenesis of permanent molars in early hominids may have followed the pattern currently observed in the lower DM2. That is, all cusps developed within a short period of time rather than showing the prolonged lag between cell division and differentiation described by Butler (1967b) as typical of modern first permanent molars. At the genetic level, this could result from minor changes in the spatial and temporal ordering of amelogenin gene expression during organogenesis (Snead et al., 1988), that is, changes in the rate of maturation of ameloblasts, and their location within the developing tooth germ. Thus, the development of the fossil permanent molar may have resembled that of the deciduous molars in spatial patterning and timing of ameloblast activity as well as fast rates of enamel apposition and extension of the mineralizing front.

CONCLUSIONS

The data presented here support the well known assumption that the DM2 is more conservative in form than the M1. The form differences between the two teeth are well established by the time the DEJ acquires its final form and increase during the later phases of enamel apposition. They are primarily due to difference in the angulation of cusps relative to one another, and appear to correlate with the known differences in the timing and rate of cell division relative to differentiation and mineralization in the two teeth. On the basis of this assumption, we infer that the resemblance found between the Skhul DM2 and M1 and the recent DM2 may indicate a similar growth pattern, and that the slow growth rate of the recent permanent molar relative to DM2 may be a relatively new phenomenon.

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